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THE EFFECTS OF VARYING ORIENTATION TO LIGHT AND WIND
ON TEMPERATURE EXCESS IN THE DRAGONFLY

Belonia saturata

A Thesis
Presented to the
Faculty of
California State University,
San Bernardino

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Biology

by
James Eric Dunn
November 1992

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Approved by:

 12-10-92

Dr. David Polcyn, Chair, Biology Date



Dr. Richard Fehn



Dr. James Ferrari

ABSTRACT

Perching dragonflies rely on postural adjustments to maximize body temperature during mid-morning basking. The effect of convective cooling and radiant heat gain was investigated in taxidermic mounts of Belonia saturata. Models were subjected to varying incident light and wind angles to determine the optimal orientation for maximizing temperature excess. Light azimuth was found to be the most critical factor in determining temperature excess, with an azimuth angle of 135 degrees from the head producing the highest temperature excess, followed by 90 and 45 degrees. Wind azimuth was also found to be an important factor in those light-wind angular relationships which allowed a choice of wind azimuths at a given light azimuth. Wind azimuth angles of 180 degrees minimized convective cooling, followed by 135 and 0 degrees. It is suggested that basking dragonflies must orient with respect to both light and wind in order to maximize temperature excess.

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INTRODUCTION

Body temperature has a profound effect on virtually every physiological process of an organism. It is therefore not surprising to find a wide range of physiological and behavioral responses to environmental temperature in the insects. In a flying insect, the ability to regulate body temperature allows the organism to be active over a wider range of ambient temperatures, therefore enhancing foraging and reproductive success. Every thermoregulatory response entails some cost, and these behaviors should reflect a compromise between the benefits and the associated costs or risks (Huey and Slatkin, 1976).

Several means of controlling body temperature have been characterized in terrestrial insects, including shuttle movements in a thermal gradient, endothermy, substrate selection and postural changes to vary the amount of radiant heat gain (reviews by Casey, 1981 and May, 1979).

Energetically, postural adjustments are among the least expensive means of regulating body temperature. Previous studies have focused on the role of solar heating, with little or no attention given to the effect of orientation with respect to wind on rates of convective heat loss. This study examines the effect of varying orientation with respect to both light and wind on body temperature in the dragonfly Belonia saturata.

AVENUES OF HEAT EXCHANGE

Several generalizations regarding the relative importance of the various avenues of heat exchange in the insects can be made. The thermal environment may affect an organism by adding or removing heat, which results in a change in body temperature, unless compensated for by evaporative heat loss or metabolic heat production (Bakken et al, 1985). For an insect to be at temperature equilibrium, the energy entering the organism must equal the energy lost by the organism.

$$\text{ENERGY IN} = \text{ENERGY OUT}$$

OR

$$A + B = \pm C \pm D \pm E$$

A = Radiation absorbed - amount reradiated

B = Metabolic energy produced

C = Energy lost or gained by convection

D = Energy lost or gained by conduction

E = Energy lost due to evaporative cooling

The equilibrium temperature of an organism is therefore increased by maximizing any term on the left side of the equation or minimizing any term on the right side of the equation.

Although evaporative heat loss has occasionally been implicated as a factor controlling body temperature in insects, under most circumstances the quantities of heat lost by evaporation are an order of magnitude or more lower than those lost by convection, and cannot be used as a sustained mechanism of heat loss (Casey, 1981). The relative importance of conduction is also negligible in most insects, because of the small area actually in contact with the substrate. Metabolic heat can be significant in flying or shivering insects, but in non-flying species, or flying species at rest, this will also be insignificant.

With insects at rest in the absence of solar radiation, the body temperature will be close to ambient, and for this reason convection (which occurs in proportion to the temperature differential) does not play much part in the heat flux (Casey, 1981). When insects at rest are exposed to sunlight, however, the heat input from solar radiation becomes a significant element in their heat balance, and body temperatures may rise far above ambient, an amount referred to as temperature excess (Digby, 1955). As substantial differences in temperature develop between the insect and its surroundings, convection becomes the major avenue of heat loss, with losses by conduction, evaporation, and long-wave re-radiation playing relatively little part (Parry, 1951).

The factors important in determining the equilibrium temperature of an insect in sunlight will, therefore, be

those that affect the rate at which heat is lost by convection (wind velocity, temperature differential, shape, size and orientation) and gained by radiation (radiant intensity, size, shape and orientation). The only factors that a basking insect has control over are orientation with respect to light and wind.

The fact that behavioral thermoregulators orient themselves to regulate the amount of radiation they receive has been extensively studied and documented (May, 1979). At low ambient air temperatures, many insects orient themselves so that the long axis of their body is perpendicular to sunlight, thus maximizing the radiant heat gained. Although the role of basking to control the rate of radiant heating is well studied in a variety of ectothermic flying insects, the role of convection cooling in the process has received less attention. Variations in posture and orientation of the body with respect to wind direction could be as important to the insect as radiation because of the importance of convection in the energy balance (Casey, 1988 and Polcyn and Chappell, 1986).

As early as 1951, Parry recognized that the temperature excess of insects in sunlight depends not only on their spatial orientation with respect to light, but also with respect to wind. Digby (1955) subjected taxidermic mounts of insects to varying wind angles in a wind tunnel and found that, in elongate cylindrical body forms, temperature excess was reduced by nearly one half by

turning them perpendicular to air flow. Since heat loss from a cylinder with air flow normal to the long axis is about twice that with the air flow in the direction of the long axis, body orientation with respect to wind should be important in determining the temperature excess of a cylindrical insect in sunlight.

In nature, orientation with respect to wind and solar radiation is not independent, but has a fixed relationship. That is, in a given environment, the organism cannot select one variable independent of the other due to the fixed light wind angle. Therefore, it may not be possible for a basking insect to maximize radiative heat gain, while minimizing convective heat loss; the orientation which produces the highest temperature excess may not be that which maximizes solar heat gain.

Polcyn and Chappell (1986) have studied the effect of varying wind and light angles on thoracic temperatures of Vanessa butterflies. They found that in most combinations of wing positions and wind velocity, temperature excess is maximized when the animal faces directly away from the wind, and minimized when the animal faces directly into the wind, regardless of light orientation. Because of the differences in body shapes and wing morphologies, and the presence of relatively dense pubescence found on Vanessa butterflies, the role of wind on convective cooling in dragonflies remains an unresolved issue.

THERMOREGULATION IN THE ODONATA

Dragonflies must attain a minimum thoracic temperature in order to fly. Some large Aeshnids are unable to fly with a thoracic temperature below 30 C (Vogt and Heinrich, 1983). May (1977) found that species capable of precise thermoregulation extend their activity periods early and late in the day while smaller, poorly thermoregulating species are restricted to midday activity. In order to remain active at low ambient temperatures, many large species must therefore maintain a thoracic temperature above ambient, and they do this by both behavioral and physiological means.

With regard to their means of thermoregulation, Corbet (1963) recognized two types of Odonata: Those which, when active, remain constantly on the wing, and those which spend most of the active period on a perch from which they make short flights. Corbet refers to dragonflies of the first type as "fliers" and those of the second type as "perchers".

May (1976) studied over two dozen species of dragonflies from Panama and Florida, detailed their elaborate behavioral and physiological means of thermoregulation, and presented evidence that both flyers and perchers regulate body temperature. May concludes that most flyers tend to rely on physiological controls such as circulatory shunts, while most perchers tend to rely on

behavioral controls such as postural adjustments to regulate body temperatures.

Fliers rely on the fact that flight generates a great deal of metabolic heat, and in the the larger species this warms the thorax faster than convection can cool it, so that a temperature excess is maintained. May (1976) demonstrated that continuously flying dragonflies regulate thoracic temperatures by controlling metabolic heat production, alternately using gliding or powered flight or controlling heat loss by altering circulation between thorax and abdomen.

Perchers are well-suited for heliothermy; since they remain stationary much of the time, they are capable of selecting small areas of favorable thermal conditions and are able to control radiant heat load by making fine postural adjustments. May (1976) demonstrated that several perching species utilize postural adjustments to regulate thoracic temperature, and perchers which were tethered in the sun, unable to alter their posture, were unable to regulate body temperature.

Studies dealing with postural adjustments have emphasized the importance of radiant heat gain in basking individuals. Tracy et al. (1979) studied the effectiveness of thermoregulatory postures in Hagenius brevistylus at varying windspeeds and air temperatures. Tests on the effect of posture on body temperature were made on both live and dead specimens in a closed circuit wind tunnel in

full sunlight. Tracy found that equilibrium body temperature is dependent upon the posture of the dragonfly relative to incoming solar radiation, but did not investigate the effect of varying wind direction on body temperature. The present study examines the relative importance of convective cooling and radiant heat gain in various positions by a single species, B. saturata.

Most perchers are diurnal and belong to the families Petaluridae, Gomphidae and Libellulidae (Corbet, 1963). These are the best known dragonflies, since they are common throughout the United States. B. saturata is a common southwestern species with an overall length of 52-61mm and an abdomen of 34-40mm.

In B. saturata it is likely that postural adjustments are used to regulate body temperature, since the species has been shown to thermoregulate by entirely exothermic means; individuals tend to be active only when the sun is shining, and Heinrich and Casey (1978) have demonstrated that individuals are unable to significantly increase thoracic temperature by shivering, and found no evidence of a physiological capacity to transfer heat between abdomen and thorax.

This species shows a relatively limited repertoire of postural positions. B. saturata never perch on the ground, but orient themselves either horizontally (at low ambient temperature) or vertically (at high ambient temperature) on the tops of vegetation or other perches.

There is also no apparent relationship between wing position and temperature since the wings are usually held horizontally or nearly so (May, 1976 and personal observation).

B. saturata demonstrates a stereotypic behavior each day. At low air temperatures (< about 26 C), individuals tend to keep their bodies parallel to the ground, and bask for long periods of time. At intermediate air temperatures (about 26-32 C), animals perch for only short periods of time and fly almost continuously. At high air temperatures (> about 35 C) which occur during midday with the sun directly overhead, the dragonflies tend to orient themselves vertically and perch on the shady portions of plant stems, presumably to minimize radiant heat gain. (Heinrich and Casey, 1978, and personal observation). At very high ambient temperatures, individuals are forced to reduce their flight activity (mating, territorial defense, feeding), possibly because they cannot dissipate excess heat from the thorax.

Although much attention has been given to the subjects of body posture and body orientation with respect to light angle in perching dragonflies, little attention has been given to the other major avenue of heat exchange - convection. This study investigates the effects of varying light and wind angles on the temperature excess of taxidermic models of B. saturata.

MATERIALS AND METHODS

The effect of varying orientation with respect to light and wind at varying wind velocities was determined using taxidermic mounts of B. saturata. Dead, dried individuals were matched for color, weight and body dimensions, and the largest available individuals were used (due to the higher thermal inertia, transient temperature fluctuations will be less pronounced). All individuals were collected at the Santa Ana River in San Bernardino, CA. The three individuals selected for use in this study were indistinguishable to the eye in terms of color, had a dry weight of $0.18 \text{ grams} \pm 0.1 \text{ g}$, and had a body length of $59.0\text{mm} \pm 3.0\text{mm}$.

Individuals were killed in a jar containing ethyl acetate, dried with wings horizontal to simulate basking posture, the legs were removed, and individuals were fitted with a copper-constantan thermocouple. Thoracic temperature was measured with a a 36 gauge copper-constantan thermocouple which was insulated with plastic tubing, inserted 3.0 mm into the center of the dorsal surface of the thorax, and anchored with glue.

Temperature excess was determined by subtracting the ambient temperature from the temperature of the taxidermic mount. Ambient air temperature was measured exactly 5.0 cm upwind from the model using 0.3 mm copper-constantan thermocouple. All temperature

measurements were determined using a Bailey BAT-12 thermocouple thermometer (volt meter) accurate to within 0.1 C, calibrated against a mercury thermometer.

The three models were placed in a free jet wind tunnel capable of generating wind velocities between 0.25 and 6.0 m/s. Specimens were subjected to wind azimuth, or horizontal, angles of 0 degrees through 180 degrees relative to the long axis of the body in increments of 45 degrees. Wind velocity was varied from 1.0-5.0 m/s, measured exactly 5 cm upwind from the models using a Thermonetics Model HT-100 hot-wire anemometer.

The light source was a 150-W incandescent lamp which could be rotated in a 180 degree arc around the wind tunnel. In order to maintain a constant radiant heat source, the lamp was maintained exactly 30.0 cm from the thorax at all times. Total incident radiation load at this distance is about 750 Watts per square meter, or about 75% of full sunlight at sea level on a cloudless day (Polcyn and Chappell, 1986). Specimens were subjected to light azimuth, or horizontal, angles of 0 degrees through 180 degrees relative to the long axis of the body in increments of 45 degrees. The zenith, or vertical, angle was maintained at 45 degrees above the horizon to simulate a typical light angle found during mid-morning basking of B. saturata.

The mean temperature excess values for the three individuals at each possible combination of light and wind azimuth was determined at wind velocities of 1, 2, 3, 4 and 5 m/s.

The effect of light angle on temperature excess, at all wind angles and wind velocities was evaluated with an analysis of variance test (ANOVA). The effect of wind angle on temperature excess, at all light angles and wind velocities was also evaluated with an analysis of variance test.

RESULTS

Figure 1 allows identification of the orientations that maximize and minimize temperature excess at a given fixed light-wind angle. In all of the fixed light-wind relationships, temperature excess is minimized when the light azimuth is 0 degrees. In most light-wind relationships, temperature excess is maximized when the light zenith is 135 degrees, with the exception of that shown in Figure 1C, where light zenith of 90 degrees produces the greatest excess, and in Figure 1D, where temperature excess is approximately the same for light azimuths of 45 degrees, 90 and 135 degrees.

Varying light azimuth influences temperature excess, with a light azimuth of 0 degrees producing the lowest temperature excess, and a light azimuth of 135 degrees producing the highest temperature excess (Figure 2).

The analysis of variance test indicates a significant effect of light azimuth on temperature excess at all wind velocities and wind azimuths ($F=58.02$; $df=4,370$; $p<0.01$).

Varying wind azimuth influences temperature excess, with wind azimuths of 45 and 90 producing the lowest temperature excesses, and a wind azimuth of 180 degrees producing the highest temperature excesses (Figure 3).

The analysis of variance test indicates a significant effect of wind azimuth on temperature excess at all wind velocities and light azimuths ($F=4.90$; $df=4,370$; $p<0.01$).

The results shown in Figures 1, 2, and 3 and the results of the ANOVA's indicate that orientation to both light and wind azimuth is important in determining temperature excess in basking B. saturata.

Figures 1, 2, and 3 also show the effect of wind velocity on temperature excess. Temperature excess is inversely proportional to wind velocity at all light-wind orientations.

Figure 1. Temperature excess as a function of light-wind angle for five possible light-wind orientations, each point representing the mean of the three test values. Each graph represents a 360 degree rotation of the individual models at a fixed light-wind angle. Graph A shows temperature excess values when light and wind are approaching from the same direction, B when they are separated by 45 degrees, C when they are separated by 90 degrees, D when they are separated by 135 degrees and E when they are separated by 180 degrees.

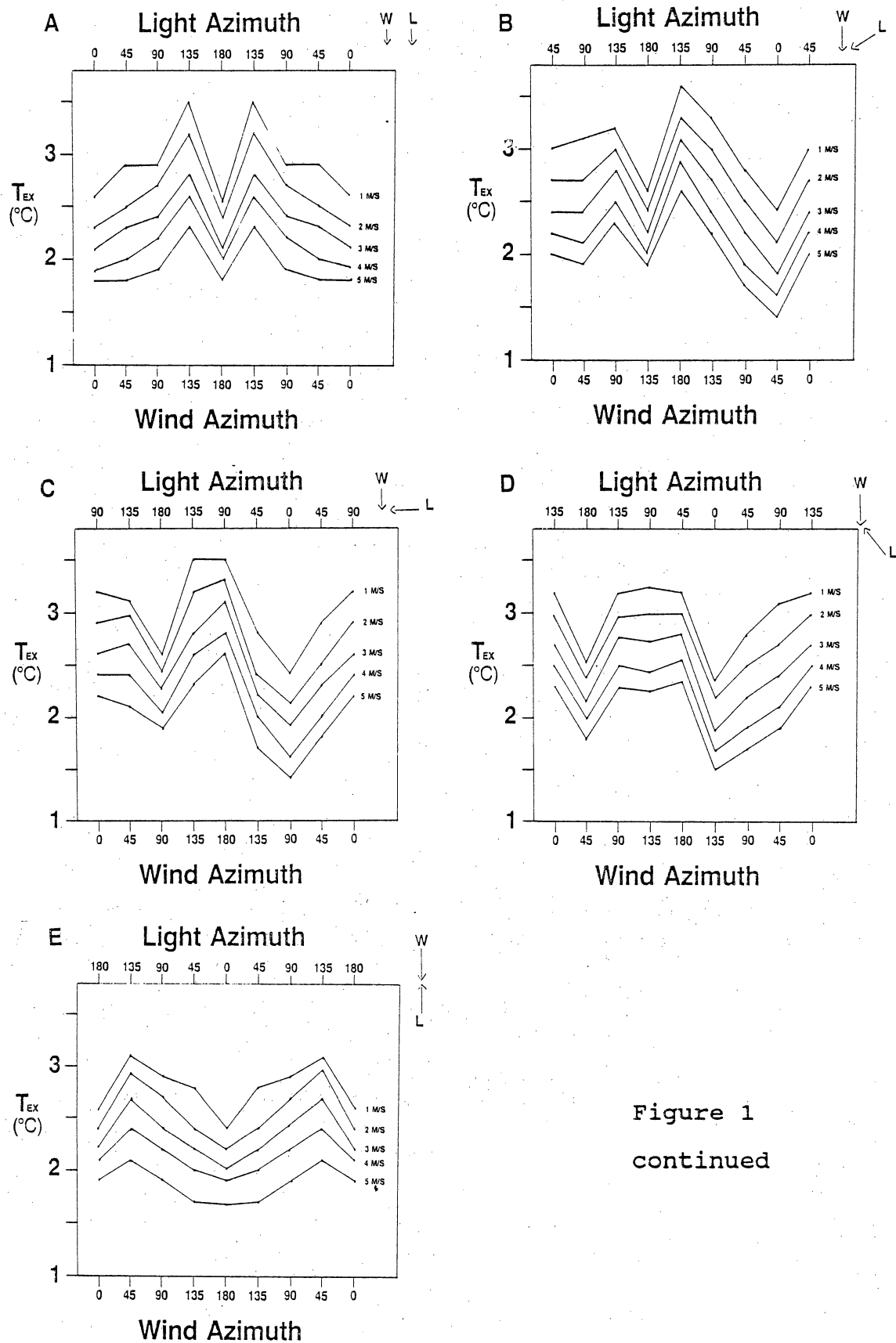


Figure 1
continued

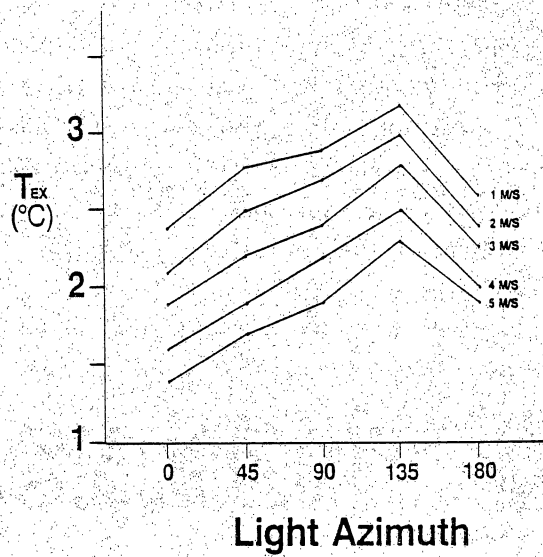


FIGURE 2
Temperature excess
as a function of
varying light
azimuth when wind
azimuth is held
constant at 90
degrees.

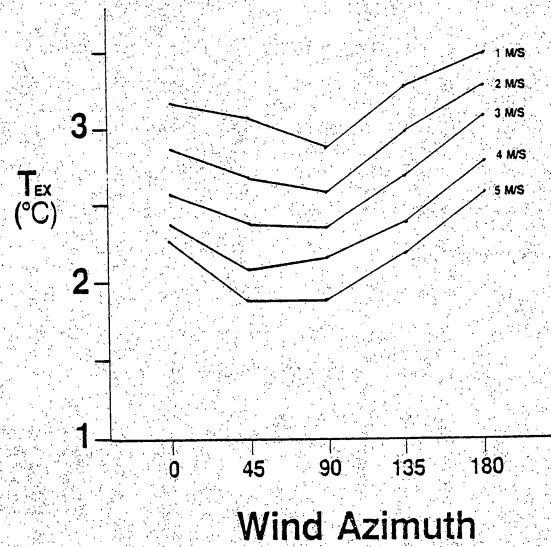


FIGURE 3
Temperature excess
as a function of
varying wind
azimuth when light
azimuth is held
constant at 90
degrees.

DISCUSSION

The control of body temperature through posturing with respect to light has been studied in many organisms. There are, however, some accepted ideas regarding posturing that have not been sufficiently investigated, such as the assumption that in order to maximize temperature excess, basking dragonflies tend to orient themselves at a 90 degree angle relative to the sun. Polcyn and Chappell (1986) have shown that orientation with respect to wind is also important in determining body temperature of Vanessa butterflies. The current study investigated the role of both convective cooling and radiant heat gain on the temperature excess of basking B. saturata.

Figure 1 indicates that light azimuth has a significant effect on the temperature excess of the taxidermic mounts. In all cases, temperature excess is minimized when light azimuth is zero degrees and is also low when light azimuth is 180 degrees, regardless of the wind angle. This agrees with the accepted view that orientation with respect to light is critical in the control of body temperature. It is significant, however, that temperature excess is not maximized at azimuths of 90 degrees as would be predicted based on inanimate cylindrical objects. In most light-wind relationships, temperature excess tends to be highest when light

azimuths are 135 degrees, suggesting that maximum radiant heat gain does not occur when radiation is perpendicular to the body. Figure 2 supports this; radiant heat gain is maximized when light approaches from an azimuth of 135 degrees, in contradiction to what would be expected based on the heating of an inanimate cylindrical object. One possible explanation is the presence of the pigmented stripes on the wings; individuals have two bands of wing pigmentation, adjacent to the body. It has been suggested that these are related to reproductive behavior, but it also appears to shade the body when light azimuth is 90 degrees and light zenith is 45 degrees (personal observation). It might be significant that such wing bands are common among perching species such as B. saturata, but are rare among flying species (D.M. Polcyn, personal communication). It would be useful to determine if removing the wings would alter the results indicated in Figure 2B.

If a dragonfly was quadrilaterally symmetrical, we would expect no difference in values for 45 and 135 degrees, and for 0 and 185 degrees, but Figure 2 also indicated a non-symetry of temperature excess for these values. The greatest solar heat gain occurs at 135 degrees, followed by 90 and 180 degrees, which are approximately equal, followed by 45 degrees, and the least gain occurs at 0 degrees. It is important to note

that the thorax and abdomen are thermally independent, and that temperature may vary significantly within the body of the individual. Heinrich and Casey (1978) have shown that a dragonfly oriented with the long axis perpendicular to solar radiation exhibited equilibrium abdominal temperatures 3 degrees lower than the equilibrium thoracic temperature. It is clear that determining the radiant heat gain of the thorax is much more complicated than simply varying the angular direction with respect to the long axis of the body in order to place it perpendicular to the sun. It is interesting to note that a light azimuth of 90 degrees and 180 degrees produce the same amount of thoracic heat gain.

Figure 1 also suggests that wind azimuth is important in determining temperature excess, since maximum values do not always occur at light azimuths of 135 and variations occur in each graph at a given light azimuth value. In Figure 1C, a light azimuth of 90 degrees produces the greatest excess, and in Figure 1D, temperature excess was approximately equal for light azimuths of 45, 90 and 135 degrees, in contradiction to what was shown in Figure 2.

Figure 3 indicates that wind azimuth is also important in determining temperature excess. Temperature excess values are maximized when wind azimuth is 180 degrees, followed by 135 and 0 degrees,

which are approximately equal, followed by 45 and 90 degrees which are approximately equal. This indicates that heat loss through convection is maximized when the body is turned perpendicular to the wind. Digby (1955) states that heat loss from a cylinder with air flow normal to the long axis is about twice that with the air flow in the direction of the long axis, but the reason for this has not been adequately investigated. It is possible that when a cylinder is parallel to the air flow, the air passing over the body equilibrates with the body temperature, and thus has less of a temperature differential to drive convective heat exchange. In contrast, a cylinder perpendicular to air flow has less distance in which the air can equilibrate, maintaining a greater differential, and thus increasing convective exchange. This effect might be amplified by the effect of turbulence, which would be greater in a cylinder perpendicular to the flow, thus increasing convective cooling.

Again, the graph in Figure 3 is asymmetrical in that 180 and 0 degrees, and 45 and 135 do not yield the same values. Perhaps wind approaching from the posterior is deflected from the thorax, yielding the higher temperature excess values obtained for 135 and 180 degrees. It would again be interesting to determine the effect of removing the wings on the results illustrated in Figure 3. Another explanation is that

temperature differential is greatest at the proximal end of the organism, allowing for greater convective exchange in this region of the body. It would be interesting to perform a set of experiments on an inanimate cylinder, taking temperatures at various regions of the object, at differing orientations to wind to determine this effect on regional body temperature.

The results shown in Figures 2 and 3 allow us to make predictions regarding the most advantageous postures for a basking dragonfly in a given fixed light-wind relationship, and should be reflected in Figure 1. In nature, the angular relation between light and wind is fixed, and any postural adjustment resulting in a change in the angle of one will result in a change in the other. It is most realistic, then, to examine the options available to an organism in a given regime.

Figure 1A shows the options available when light and wind are approaching from the same direction. Temperature excess is maximized when light azimuth is 135 degrees and wind is 135 degrees ($T_{ex}=3.5$ C at $V=5$ m/s). The other light azimuth which produces a high temperature excess (90 degrees) is negated by a wind azimuth of 90 degrees, which acts to minimize temperature excess. The lowest temperature excess ($T_{ex}=2.5$ C at $V=5$ m/s) occurs when light and wind azimuth is 180 degrees. Thus, a change in angle of only 45 degrees can produce a change in body

temperature of 1 degree Celsius.

Figure 1B shows the options available when light and wind are separated by 45 degrees. This situation would be most advantageous since it allows for posturing which maximizes temperature excess. Body temperature is maximized when light azimuth is 135 degrees and wind azimuth is 180 ($T_{ex}=3.6$ C at 5 m/s). This is the highest value obtained in this study, and could be predicted based on the results shown in figures 2 and 3, which show the highest radiant heat gain at 135 degrees and the least convective cooling at 180 degrees. Body temperature is minimized when light azimuth is 0 degrees and wind azimuth is 45 degrees ($T_{ex}=2.4$ C at 5 m/s). This is the lowest value obtained in this study, and is expected since radiant gain heat is minimal at 0 degrees, and convective cooling is maximal at 45 degrees.

Figure 1C shows the options available when light and wind are separated by 90 degrees. In this case temperature excess is maximized when light azimuth is 90 degrees and wind azimuth is 180 degrees ($T_{ex}=3.5$ C at 5 m/s), although light azimuth of 135 degrees and wind azimuth of 135 degrees produce a value almost as high. Presumably the difference in radiant heat gain from 135 degrees is offset by the minimal convective cooling occurring at 180 degrees. Body temperature is minimized when light azimuth is 0 degrees and wind azimuth is 90 degrees.

Figure 1D shows the options available when light and wind are separated by 135 degrees. In this case, there are no clear peaks indicating the most advantageous posture; the effects of increasing radiant heat gain are offset by increasing convective cooling, and the light and wind azimuths of 135 and 0, 135 and 90, 90 and 135, and 45 and 180 all produce similar body temperatures (T_{ex} about 3.2 C at 5 m/s). The organism has more options available for maximizing body temperature, but there is a single orientation which minimizes temperature excess, light at zero degrees and wind at 135 (T_{ex} =2.3 C at 5 m/s).

Figure 1E shows the options available when light and wind are separated by 180 degrees. If the organism was symmetrical, we would expect this graph to be identical to graph A, but the shift in the peak values toward light azimuth of 135 degrees and wind azimuth of 45 degrees (T_{ex} =3.1 at 5 m/s) indicate the noted asymmetry. Body temperature is minimized when light azimuth is 0 degrees and wind azimuth is 180 degrees (T_{ex} =2.4 at 5 m/s). This is interesting because at wind azimuth of 180 degrees, convective cooling is minimal, again indicating the importance of radiant heat gain.

These results indicate that temperature excess of a basking dragonfly is a complex function of both wind and light azimuth angles. Light azimuth seems to be the more significant factor, since peak temperature excess

always occur when light azimuth is 135 degrees, or in some cases, 90 and 180 degrees. However, in certain light-wind relationships, wind can play an important role in dictating the most advantageous posture.

In Figures 1A and 1E, Temperature excess is maximized by simply turning the body to a light azimuth of 135 degrees. In Figure 1B, however, there are two choices for selecting a light azimuth of 135 degrees: one with a wind azimuth of 90 degrees, and one with a wind azimuth of 180 degrees. The difference in temperature between these is 0.4 C, a difference which could be quite significant to a basking individual. This is also true in Figure 1C, where light azimuths of 135 degrees are paired with wind azimuths of either 45 or 135 degrees, resulting in a 0.4 C difference. In Figure 1D, the temperature difference with a light azimuth of 135 degrees and wind azimuths of 0 and 90 degrees does not produce a large temperature difference.

In conclusion, light azimuth is the most important factor influencing temperature excess of basking B. saturata, with azimuth angles of 90, 135, and 180 degrees maximizing radiant heat gain, but wind azimuth is also a significant factor, with wind azimuths of 45 and 90 degrees minimizing convective heat loss. In certain light-wind angular relationships, it would be important for basking individuals to select the proper orientation to both light and wind. Observation of basking

dragonflies in the field reveals constant minor adjustments in the angular relation to light and wind, and presumably the individuals are seeking the optimum posture to maximize temperature excess. It would be interesting to study basking dragonflies in the field, and to determine if the findings of this study could be used to predict the posturing behavior under a given set of environmental conditions.

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